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Research Article

Seek and you shall find: Detection of alien bryozoans along the Chilean SE Pacific coast with a simple and cost-efficient methodology

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Abstract

Invasions by non-indigenous species (NIS) are among the major problems that coastal ecosystems are facing globally and are driven by anthropogenic activities, such as international vessel traffic and aquaculture. Bryozoans are typical constituents of vessel hull-fouling communities, and the phylum contains several notorious globally invasive species. Few NIS, including bryozoan species, are reported along the Chilean Southeast Pacific coast, which has traditionally been attributed to the local oceanographic and ecologic conditions. However, the low numbers may also be the consequence of insufficient monitoring, as well as the small size and morphologic similarity of many species, which hinders their detection. Here, we deployed artificial floating settlement plates in strategic locations (ports/marinas or aquaculture sites) along the Chilean coast (from 29°S to 41°S), to detect non-indigenous bryozoans. With this method, we found a total of 14 species, including five NIS and four cryptogenic species. Additionally, we report two NIS from opportunistic findings in the rocky intertidal zone and from a piece of plastic litter. Three species represent new records from Chile: *Bugulina* cf. *fulva*, *Bugulina stolonifera*, and *Watersipora arcuata*. These are described in detail in the present paper. The new records importantly enhance the number of known (bryozoan) invasions along the Chilean coast and corroborate the need for regular monitoring. The installation of artificial settlement plates at high-risk sites (especially ports and marinas) has proven to be a successful and efficient low-cost approach, which can help to detect NIS introductions in their early stages, before spreading to natural environments. Regular monitoring of these sites, as well as compulsory legislation for hull cleaning, both for long-distance (nationally and internationally) travelling and local vessels, could greatly reduce the problem.

Key words: Bryozoa, hull fouling, marine invasions, non-indigenous species, settlement plates, Southeast Pacific

Introduction

Non-indigenous species (NIS) are a global concern due to their effects on native communities, global biodiversity, and human livelihoods (Pyšek et al. 2020). Several anthropogenic vectors transport these species across the world's oceans to new coastal habitats. Amongst those, vessel traffic seems to be the quickest and most successful form of transport for sessile fouling species (e.g., Seebens et al. 2013; Ruiz et al. 2015; Carlton et al. 2019), introducing them to port areas around the world. Outside the main shipping routes, floating marine litter is also important, as it disperses with oceanic currents and reaches even very remote locations (Kiessling et al. 2015; Rech et al. 2021, 2023).

Bryozoans are among the most frequent groups of maritime hull-fouling organisms (e.g., McCann et al. 2019; Rech et al. 2024a). Some bryozoan NIS are already widespread and reported from many parts of the world, where their ability to foul large surfaces makes them a nuisance and a threat (e.g., Nascimento et al. 2022). However, inter-species phenotypic similarity, intra-species phenotypic plasticity, and historic taxonomic confusion hinder the detection and identification of many bryozoan NIS. Some of them can be distinguished only through elaborate *ex-situ* analyses, like scanning electron microscope (SEM) imaging or genetic barcoding, and they are easily overlooked or confounded with similar species in field surveys. Moreover, most of the world's coastal regions are severely understudied and have no regular monitoring in place. Recent studies in otherwise poorly sampled locations found that non-native bryozoans and even undescribed species are relatively common in such regions. For example, Vieira et al. (2012) described 9 new species of Bugulidae from four understudied regions of the Brazilian coast, based on manual samplings. Similarly, Rech et al. (2024a) recently published the first record of the widespread fouling species *Watersipora subtorquata* on remote Rapa Nui (Easter Island), based on a four-month settlement plate-based survey.

In the past, the South American Pacific coast has been proposed to be relatively "more pristine" or more resistant to bioinvasions than other global regions, due to the small number of high-impact NIS found there (Castilla and Neill 2009). However, a reliable estimation of NIS frequency along the SE Pacific coastline is not possible due to a lack of sampling and regular monitoring, meaning that actual numbers of NIS are probably much higher than those reported (Carlton 2009; Stowhas et al. 2023). Castilla et al. (2005) and Castilla and Neill (2009) listed only two bryozoan NIS in the Eastern South Pacific: *Bugulina flabellata* and *Bugula neritina*. Another NIS, *Cryptosula pallasiana*, was reported from aquaculture buoys in the northern-central Coquimbo region (Astudillo et al. 2009). Moreover, Leclerc et al. (2018, 2020a, b) recently reported seven additional non-indigenous or cryptogenic species (*Alcyonidioides mytilii*, *Amathia* cf. *gracilis*, *Amathia* cf. *imbricata*, *Cauloramphus spiniferum*, *Conopeum reticulum*, *Electra monostachys*, and *Exochella* n. sp.) from surveys in Southern Chilean ports, and Rech et al. (2024a) reported the globally invading NIS *W. subtorquata* from Rapa Nui (Easter Island).

In contrast to many other taxa, the Chilean bryozoan fauna is well investigated and described, largely thanks to the work of Hugo Moyano, who studied the phy-

lum for more than 3 decades (from the early 1970s to the early 2000s). Despite his extensive studies, the author reported only two bryozoan NIS, *B. neritina* and *B. flabellata* (Moyano 1982, 1991), from Chile. On the one hand, this could suggest that most bryozoan invasions along the Chilean coast are indeed recent (i.e., from the last 20 years). On the other hand, Moyano's studies focused on natural marine habitats, whereas recently reported NIS were found in ports and/or on artificial surfaces (Rech et al. 2018, 2024a; Leclerc et al 2018, 2020a, b), highlighting the importance of these locations and substrata as entry points and propagule reservoirs for marine NIS. Moreover, Moyano´s comprehensive description of the Chilean Bryozoa is based on the study of specific habitats and sites at specific points of time and does not represent a regular monitoring of the 2000 km of Chilean coastline, which comprises a large variety of coastal habitats, both natural and artificial.

Chile has a long history of international vessel traffic, with 39 international ports and more than 5000 ship arrivals per year (Stowhas et al. 2023), as well as about 20 marinas (https://www.harbourmaps.com/en/harbours/region/chile). Such local harbours are known to play an important role in secondary NIS dispersal (e.g., Ashton et al. 2022a). Several of the non-indigenous bryozoans reported from Chile so far are known for fouling ship hulls (e.g., Gollasch 2002; Ramalhosa et al. 2017). Moreover, some of them are known to attach to floating debris, which may also be important for secondary dispersal along the Chilean coast (Rech et al. 2023). Another vector for NIS introductions is the intentional or unintentional release from aquaculture facilities. While regulation of this sector has led to decreases in NIS introductions in, for example, Europe and California (Katsanevakis et al. 2013; Williams et al. 2013), existing policies seem to be insufficient or ineffective in Chile (Camus 2005; Stowhas et al. 2023). In addition to the organisms directly released from aquaculture sites, NIS can also be dispersed when aquaculture equipment and gear is intentionally moved (e.g., Iacarella et al. 2019) or accidentally lost from the farming sites (e.g., Astudillo et al. 2009; Campbell et al. 2017; Beermann et al. 2025).

Considering all the above, we hypothesized that undetected or overlooked bryozoan NIS are probably present in high-risk sites associated with international, national, and local vessel traffic and/or aquaculture along the Chilean coast. Therefore, the goal of the present study was the detection and identification of such NIS with a simple and well-tested settlement plate-based approach (e.g., Tamburini et al. 2021). Apart from this observational approach, we report additional new findings of Bryozoa NIS from Chilean coastal sites.

Methods

Study region

The study was conducted along the Southeast Pacific Ocean, covering the Chilean continental coast from 29°S to 41°S and Rapa Nui (Easter Island, 27°S, 109°W). Rapa Nui is situated about 4000 km offshore and is connected to the continent via the currents of the South Pacific Subtropical Gyre and regular vessel traffic (Fig. 1). Plate-based settlement surveys were conducted at six strategic locations (ports/yachting clubs and/or aquaculture sites; Suppl. material 1: table S1). On Rapa Nui, we chose the main port, Hanga Piko (27.15°S, 109.43°W) that harbours local fishing boats and barges, used to fetch goods from ships at the offshore an-

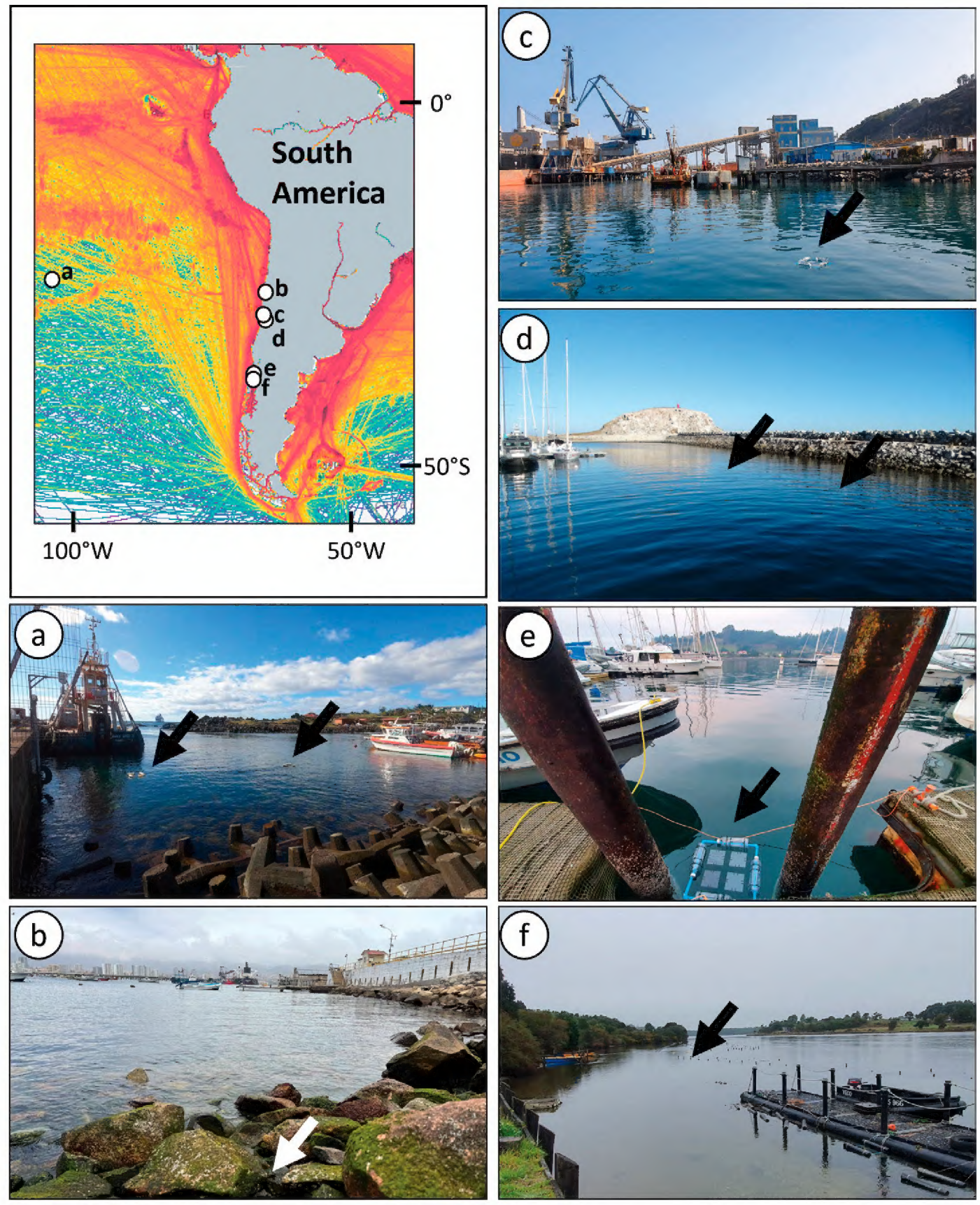

Figure 1. Study region with density map of total vessel traffic (year 2023), ranging from 1 (blue) to > 5000 (dark red) routes * 9.78 km^{-2} $year^{-1}$. Source: https://www.marinetraffic.com/. Study sites are indicated with letters: **a.** Rapa Nui (Easter Island), Hanga Piko harbour. Photo credit: Pamela Averill. **b.** Coquimbo Bay. Photo credit: Martina Cacciuttolo-Said. **c.** San Antonio International Port. Photo credit: Sabine Rech. **d.** Algarrobo, Cofradía Náutica del Pacifico. Photo credit: Mariano Galdames Beckdorf. **e.** Puerto Montt, Yachting Club Reloncaví. Photo credit: Sabine Rech. **f.** Ancud, Quempillén Research Station. Photo credit: Sabine Rech. Black arrows point to floating frame with settlement plates (not visible in pictures **b, d** and **f**). White arrow indicates the site where *Watersipora arcuata* was found invading the rocky seafloor at the Coquimbo site.

chorage site for cruise ships and commercial vessels, located about 500 m offshore. On the continental coast, our northernmost study site was a small aquaculture concession (29.97°S, 71.35°W), belonging to the campus of Universidad Católica del Norte in the protected Coquimbo Bay. Adjacent to the site is the local fishing port of Guayacán and the anchorage site for large commercial vessels associated with the local iron mining industry (vessel can be seen in Fig. 1b). In the central region of the Chilean coast, settlement plates were installed in the International Port of San Antonio (33.58°S, 71.62°W) and at a local yachting club (33.36°S, 71.69°W), both of which are situated directly on the exposed coastline, protected

only by breakwaters. In the southern region, our study sites were in Puerto Montt and Ancud and were not directly exposed to the sea. Puerto Montt is located on the coast of the Inner Sea of Chiloé. There, settlement surveys were conducted at a yachting club (41.49°S, 72.99°W) located in a narrow fjord. In Ancud, settlement plates were installed close to a small aquaculture concession, located in the Quempillén River estuary (41.87°S, 73.78°W).

Sampling approach

Settlement plates were installed between February and November 2022. If possible, settlement surveys were conducted twice, once in the austral spring/summer and once in the austral autumn/winter, at each site. However, due to limitations related to the COVID19 pandemic, they could only be carried out in one season at Hanga Piko and San Antonio. Settlement plates were deployed for 4 months per season at each site. The exact dates of installation and retrieval are specified in Table S1. At each location, two floating units, each containing four 13.5 × 13.5 cm^2 polyvinylchloride (PVC) settlement plates inside of a PVC frame, were installed at a protected site (marinas/ports or aquaculture installations; see previous section "study region"). After 4 months of immersion, plates were retrieved swimming or from a boat. For a more detailed description of the floating units and sampling protocols, please see Rech et al. (2024a). In the port of San Antonio, only one floating structure (= 4 settlement plates) could be retrieved, while the second structure was lost in a storm event. At all other sites, both structures (= 8 settlement plates) were successfully retrieved. At each study site, a first analysis, including taking photos and creating a preliminary species/taxon list, was performed in a nearby field laboratory. In agreement with other plate-based settlement studies (e.g., Ashton et al. (2022b), all analyses were only conducted on the lower (= seafloor-facing) side of the plates, as the fouling fauna was almost exclusively concentrated on this side. After the preliminary analysis, plates and their attached epifauna were preserved in 95% ethanol and transported to the marine biology laboratory at the Marine Science Faculty of Universidad Católica del Norte in Coquimbo. There, plates were immediately frozen and stored at -20 °C.

For subsequent analyses, plates were thawed, and the attached fouling community, which was often very abundant and consisted of several phyla (Suppl. material 1: fig. S1, data not published), was analysed and identified to the finest possible level with a dissecting microscope while still attached. The extensive communities had to be analysed and characterised within a limited time frame, due to the rapid decomposition of the larger soft-bodied animals (e.g., solitary ascidians). In consequence, smaller specimens of similar-looking species like *Bugulina* cf. *flabellata* and *Bugulina stolonifera* could not always be distinguished immediately and were recorded as Bugulidae spp. If the fouling cover on settlement plates was very abundant, which was the case at several continental study sites, the dense upper layers of biofouling were analysed first and carefully removed before species/specimens on the ground of the settlement plate could be detected. Samples of each distinguishable taxon were taken for each study site and season (but not from each plate at each site) and stored in 95% ethanol. Samples containing bryozoans were then searched for previously unidentified species, which were separated and identified as described below.

In addition to the species found on settlement plates, two additional species of invasive bryozoans were found opportunistically: One species was found in the

local intertidal of the university campus of Universidad Católica del Norte in Coquimbo and another one was identified on a piece of plastic litter from an earlier study (Rech et al. 2023).

All samples were analysed via light microscope (LM), scanning electron microscope (SEM), and/or DNA barcoding (see below). Species were first tentatively identified morphologically, using a dissecting microscope, and from LM images, and their identity was confirmed based on SEM images and DNA barcoding. The remaining ethanol-preserved colony fragments were deposited in the zoological collections of the Faculty of Marine Sciences at Universidad Católica del Norte in Coquimbo, Chile (SCBUCN; see Suppl. material 1: table S2 for details and museum codes). Measurements were made from SEM or LM images, using the ImageJ software (Schneider et al. 2012). Specimens from the bryozoan collection at the Natural History Museum, London (NHMUK) and the Smithsonian National Museum of Natural History (USNM) were used for comparison with our samples.

SEM analyses

For SEM analysis, the samples were dried in an oven at 40 °C for 24 hours, mounted on slide glasses using double-sided carbon tape and coated with gold in a JEOL JFC-100 evaporator. The specimens were photographed under a JEOL IT300LV SEM in the Microscopy Laboratory of Universidad de Chile, Santiago, Chile.

DNA barcoding

DNA was extracted using DNeasy Blood & Tissue Kit (Qiagen®). A segment of the cytochrome *c* oxidase subunit I (COI) gene was amplified using the universal primers HCO2198 & LCO1490 (Folmer et al. 1994). Polymerase chain reaction (PCR) was performed with the following reagents and quantities: ~ 50 ng of DNA, 1X PCR buffer (ThermoPol buffer, New England BioLabs), 2 mM $MgCl_2$, 0.6 µM of each primer, 0.25 mM of each dNTPs, 1U of Taq polymerase (New England BioLabs), and 0.06 mg mL^{-1} of Bovine Serum Albumin (BSA). PCR cycles were performed on an DLAB (TC1000-G) Thermal Cycler, under the following conditions: 94 °C for 3 min, followed by 40 cycles of 94 °C for 30 s, 55 °C for 30 s, 72 °C for 60 s, and a final extension at 72 °C for 10 min. PCR amplification was verified using 1% agarose gels. Sanger sequencing was performed by Macrogen in Santiago, Chile, using the same primers. DNA sequences were analysed with Geneious Prime® 2023.2.1 and compared against the Genbank database, using the online BLAST function (https://blast.ncbi.nlm.nih.gov/Blast.cgi). Matching sequences were validated, and only sequences corresponding to articles published in scientific journals, identified by internationally renowned taxonomists, and with a specimen voucher were considered. The DNA barcodes were deposited in the Genbank database (accession numbers PP109395–PP109397) and can also be found in the supplement.

Statistical analyses

Species richness and community composition in settlement plate-based surveys were calculated based on the presence/absence of each of 12 distinguishable bryozoan taxa: Bugulidae spp. (including *Bugulina* cf. *flabellata* and *B. stolonifera*), Ctenostomatida sp. (including *Amathia* cf. *gracilis*), *Bugula neritina*, *Cryptosula pallasiana*,

Cheilostomatida sp., Alcyonidiidae sp., *Scruparia ambigua*, *Celleporella* cf. *hyalina*, *Conopeum* sp., *Exochella* sp., *Lagenicella variabilis*, and *Watersipora subtorquata*. Species richness was calculated as the total number of species per independent sampling unit (= floating frame, n = 2 frames per combination of site and season, except for San Antonio, where n = 1, see section "sampling approach" above). Species composition was defined by the percentage of settlement plates fouled by each species per sampling unit at each combination of site and season.

Species richness and composition were compared between seasons (summer, winter; fixed factor) and sites (Coquimbo, Algarrobo, San Antonio, Puerto Montt, Ancud, Rapa Nui; fixed factor), using permutational ANOVA (PERMANOVA). The test was based on an Euclidean distance matrix for richness. For species composition, it was based on a Bray-Curtis similarity matrix, after excluding both samples from the Ancud site in winter, as they carried no bryozoans. PERMANOVA was run with a permutation of residuals under a reduced model as permutation method, sums of squares type III, and 9999 permutations, using the PERMANOVA+ function (Anderson et al. 2008) of the software Primer6 (Clarke and Gorley 2006). Non-metric multidimensional scaling was applied to a Bray Curtis similarity matrix, based on the average frequency of each species for each combination of study site and season, after excluding samples from the Ancud site in winter (no bryozoans present), and from Rapa Nui (no common species with any other study site).

Results

Settlement plate-based surveys at strategic sites along the Chilean coast resulted in the detection of 14 species of Bryozoa, including five non-indigenous, four cryptogenic, one native, and several unidentified species (Table 1). Non-indigenous bryozoans were found at all study sites, except for the estuarine location on the southern Chilean inner coast (Ancud; see Table 1). The previously unreported *B. stolonifera* was identified from three study sites, reaching from the northern to the southern region (Table 1). Another previously unreported species, *Bugulina* cf. *fulva*, was found attached to some ethanol-preserved samples of other Bugulidae from plates at the Coquimbo site, during a dedicated examination of those samples. Given the very small size of the specimens (~5 mm) and their often epibiontic growth on similar-looking bugulid species, it cannot be excluded that this species has also been present in other locations. Interestingly, there was no concordance in species occurrence between the Chilean continental coast and oceanic Rapa Nui, where only one species, the NIS *W. subtorquata*, was found on settlement plates (results published in Rech et al. 2024a).

Species richness was highest at the yachting club of Puerto Montt in both seasons (6.5 $\pm$ 0.7 and 6.0 $\pm$ 0.0 species in winter vs. summer; Suppl. material 1: fig. S2). In winter, the lowest species richness was found at the estuarine site in Ancud, where no bryozoans had attached to the plates. In summer, the lowest species richness was recorded on plates in the Hanga Piko harbour of Rapa Nui, where only one bryozoan species was found. Richness was strongly influenced by site, and with a weaker effect by season, and the interaction of both factors (PERMANOVA, $p \leq 0.0003$ for each factor, see Suppl. material 1: table S3), but no overall latitudinal pattern was observed (Suppl. material 1: fig. S2). Community composition varied between study sites and, to a much lesser extent, due to the interactive effect of study site and season (PERMANOVA, $p < 0.05$ for each factor; Suppl. material 1: table S3), but season alone had no overall effect. While oceanic

Table 1. Bryozoan species found at each study site. ✓ = species present. nd = no data, opportunistic record. Cryp = cryptogenic, NIS = non-indigenous species, nat = native. Previous records: 1 = Leclerc et al. 2018; 2 = Moyano 1991; 3 = Astudillo et al. 2009; 4 = Rech et al. 2024a. * = classified as "native" in Leclerc et al. (2018). Bold writing = first records from Chile.

		Hanga Piko (27°S)	Coquimbo (29°S)	Ritoque (32°S)	Algarrobo (33°S)	San Antonio (33°S)	Puerto Montt (41°S)	Ancud (41°S)
a) Standardized surveys: Settlement plates								
Alcyonidiidae sp.				nd			✓	✓
Amathia cf. *gracilis*[1]	cryp		✓	nd		✓	✓	✓
Bugulina cf. *flabellata*[2]	NIS		✓	nd	✓	✓	✓	
Bugulina* cf. *fulva	cryp		✓	nd				
Bugula neritina[2]	NIS		✓	nd	✓	✓	✓	
Bugulina stolonifera	NIS		✓	nd		✓	✓	
Celleporella cf. *hyalina*[1]	cryp			nd				✓
Cheilostomatida sp.				nd			✓	
Conopeum sp.				nd				✓
Cryptosula pallasiana[3]	NIS		✓	nd	✓		✓	
Exochella sp.				nd	✓			
Lagenicella variabilis	nat		✓	nd				
Scruparia ambigua[1]*	cryp			nd			✓	
Watersipora subtorquata[4]	NIS	✓		nd				
b) Additional: Natural intertidal								
Watersipora arcuata	NIS	nd	✓	nd	nd	nd	nd	nd
c) Additional: Stranded plastic litter								
Electra monostachys[1]	NIS	nd	nd	✓	nd	nd	nd	nd

Rapa Nui shared no species with any other site, the estuarine site in Ancud had the most dissimilar community composition among the continental sites (Suppl. material 1: fig. S3, table S4).

Non-indigenous and cryptogenic species dominated the fouling Bryozoan communities: Bugulidae spp. (identified in several samples as *Bugulina* cf. *flabellata* and/or *Bugulina stolonifera*) had the highest average abundances across all sites and seasons, fouling 69 ± 48% of settlement plates. They were followed by the cryptogenic Ctenostomatida sp. (identified in several samples as *Amathia* cf. *gracilis*; average abundance: 55 ± 50%) and by *Bugula neritina* (average abundance: 40 ± 47%, Suppl. material 1: table S4). The only native species, *Lagenicella variabilis*, was only identified on one settlement plate at the Coquimbo site in summer. In addition to the species growing on settlement plates, two more NIS were found opportunistically: *Watersipora arcuata* was detected by students of the Marine Biology Faculty in the intertidal zone at the university campus of Universidad Católica del Norte in Coquimbo. *Electra monostachys* had been found on two pieces of plastic litter in a previous study carried out at Ritoque beach (Rech et al. 2023), but was only recently identified at species level.

Of the eleven non-indigenous/cryptogenic species reported in the present work, two (*Bugula neritina* and *Bugulina* cf. *flabellata*) are commonly found along the Chilean coast and have been reported there since the early 1980s (Moyano 1982). Five other species, *Amathia* cf. *gracilis*, *Celleporella* cf. *hyalina*, *Cryptosula pallasiana*, *Electra monostachys*, and *Scruparia ambigua* have been reported in previous

studies from Chilean ports (Leclerc et al. 2018; 2020b). *Scruparia ambigua* had been treated as native to Chile in Leclerc et al. (2018, 2020a, b) but, given that the native range of this cosmopolitan species is not unequivocally resolved, we follow the classification of Schwindt et al. (2020), who classify it as cryptogenic even in the Southwest Atlantic, from where it was originally described (d´Orbigny, 1841). SEM images were obtained from *E. monostachys* and are shown in Suppl. material 1: fig. S4. Finally, three of the species found here (*Bugulina* cf. *fulva*, *Bugulina stolonifera*, and *W. arcuata*) represent first records for Chile. Detailed descriptions and (SEM) images of these species are presented below.

Systematic Account

Family Bugulidae (Gray, 1848)
Genus *Bugulina* (Gray, 1848)

***Bugulina stolonifera* (Ryland, 1960)**

Bugula stolonifera Ryland 1960: 78, fig. 6; Prenant and Bobin 1966: 541, fig. 158 XII, 159 II, 187; Ryland and Hayward 1977: 170, fig. 82; Hayward and Ryland 1998: 228, fig. 72; Gordon and Mawatari 1992: 23, Plate 6a; Scholz et al. 2003; Chimenz Gusso et al. 2014.
Bugulina stolonifera: Fehlauer-Ale et al. 2015; Ramalhosa et al. 2017: 9, fig. 7.

Material analyzed. Colonies from settlement plates (frozen at -20 °C) on floating devices. UCN university campus, Coquimbo, Chile (29.97°S, 71.35°W), **SCBUCN-8176**, Genbank PP109395, ID COQWINBX20230712_02 (Fig. 2), collected 22 June 2022; **SCBUCN-8177**, Genbank PP109396, ID COQ1_13.09/COQSUMBS (Fig. 2), collected 7 February 2023. San Antonio International port, Chile (33.58°S, 71.62°W), **SCBUCN-8178**, ID SANBX01 (Fig. 3), collected 18 September 2022. Club Náutico Reloncaví, Puerto Montt, Chile: **SCBUCN-8179**, ID PMSUMBX20230712_01 (Fig. 3), collected 23 January 2023.

Comparative material analyzed. NHMUK 1959.3.18.1, *Bugula stolonifera* Ryland, 1960, holotype, Swansea Docks, UK.

Characterization. Colony erect, tufted, whitish in colour, biserially branching, with bifurcation type 4 (see Ryland 1960). Specimens rather small, maximum height of 2.5 cm. Zooids long, with length and width varying between specimens from different locations (for measurements see Suppl. material 1: table S5). Distal zooid with one inner and two outer spines. Pedunculate avicularia dimorphic, present at the outer side of the zooids, slightly longer than zooid width, but smaller ones can be found at bifurcations (Fig. 2c, d), with down-curved beak (Figs 2e, 3d), about 1.5 to 2 times as long as wide (Suppl. material 1: table S5). Ovicells subglobular, 0.6–0.7 times as long as wide, centered in midline, distinct, with frontal membranous area (Fig. 2c, d).

Remarks. The specimens often co-occurred with the congener *Bugulina* cf. *flabellata* and may have been confounded with the prior species in past rapid assessment surveys in the field. *Bugulina stolonifera* had not been reported from the Southeast Pacific coast so far; it is known, however, from the Galapagos Islands (McCann et al. 2019). COI sequences of our specimens (Suppl. material 1: table S6) from Coquimbo match verified records from Spain (Fehlauer-Ale et al. 2015),

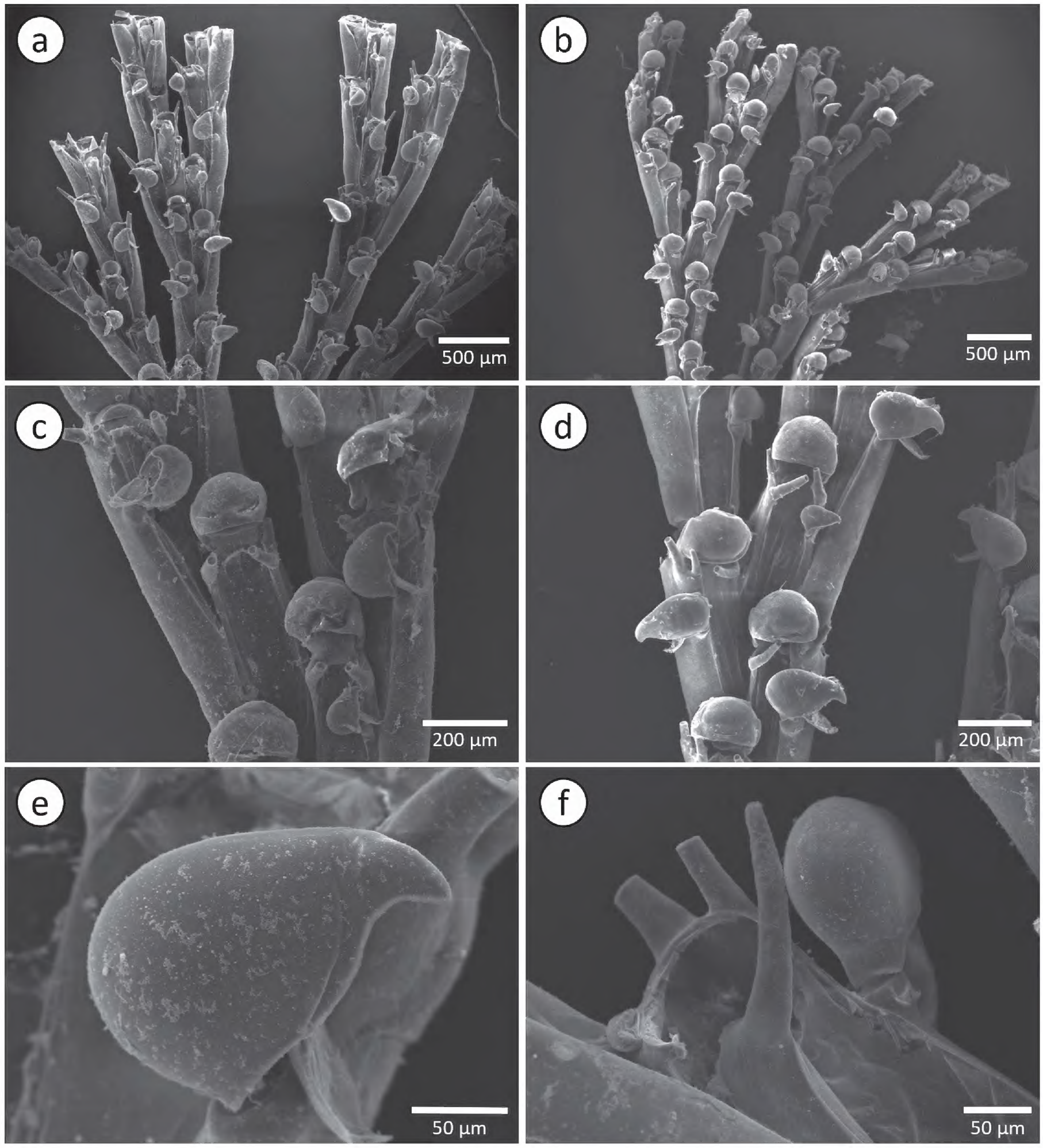

Figure 2. *Bugulina stolonifera* from Coquimbo. Samples SCBUCN8176 (**a, c, e, f**) and SCBUCN8177 (**b, d**). **a, b.** Colony overview; **c, d.** Close-up of zooids; **e.** Avicularium; **f.** Distal end of the zooid, showing three oral spines (one inner and two outer spines).

France (Couton et al. 2019) and the US Atlantic (McGovern and Hellberg 2003) and US Pacific coast (Davidson and Haygood 1999; Suppl. material 1: table S7). However, given the wide geographic range of matching sequences, we cannot draw conclusions about the origin of our specimens.

Bugulina cf. *fulva* (Ryland, 1960)

?*Bugula fulva* Ryland 1960: 86, figs 1D, 2H, 10A, B, pls. 1D, 2B. Hayward and Ryland 1998: 218, fig. 67.
?*Bugula aquilirostris* Ryland 1960: 89, fig. 12A, B.

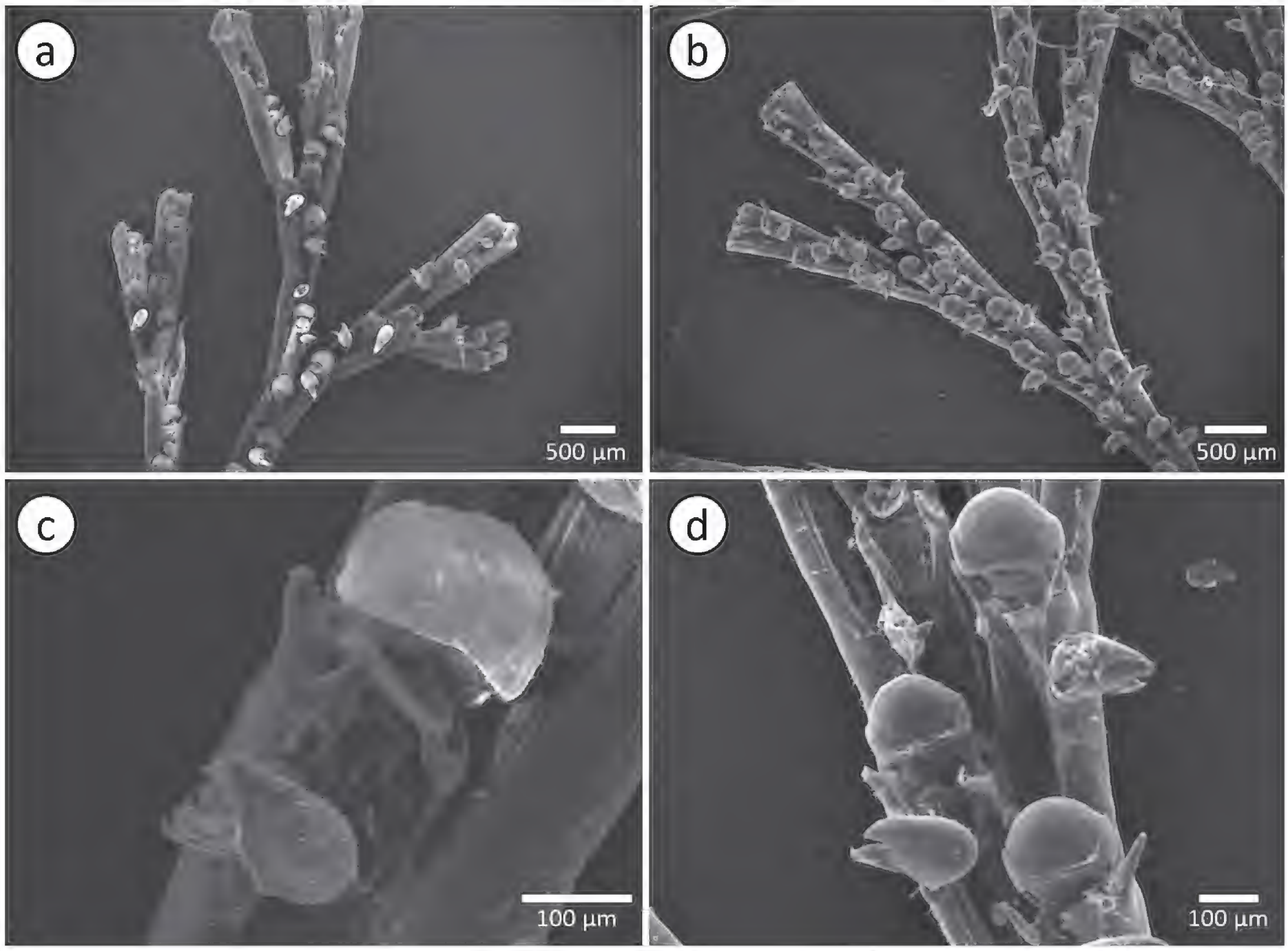

Figure 3. *Bugulina stolonifera* from San Antonio, Sample SCBUCN8178 (**a, c**) and from Puerto Montt, Sample SCBUCN8179 (**b, d**). **a, b.** Colony overview **c, d.** Close-up of zooids with avicularia, ovicells and distal spines.

Material analyzed. 6 specimens from settlement plates (frozen at -20 °C) on floating devices at UCN university campus, Coquimbo, Chile (29.97°S, 71.35°W), **SCBUCN 8180**, ID COQSUMBX04 (Figs 4, 5) and ID COQSUMBXS4 (Fig. 6), collected 7 February 2023.

Comparative material analyzed. NHMUK 1959.3.18.5, *Bugula fulva* Ryland, 1960, holotype, J.S. Ryland leg., Menai Bridge pier, Wales. **NHMUK 1959.1.20.1**, *Bugula aquilirostris*, Ryland, 1960, holotype, Bournemouth, England.

Characterization. Several small specimens (about 5 mm in height, Fig. 4) found growing on colonies of *Bugulina stolonifera* and *Bugula neritina*. Colonies biserial. Zooids long (see measurements in Suppl. material 1: table S8); gymnocyst occupying about 2/3 to 3/4 of zooid length. Three large distal spines on both the outer and inner angle (Fig. 5a); zooids may have 1–2 inner (below the avicularium) and 1–3 outer marginal spines at the proximal third of the opesial margin, with these proximal spines overarching the frontal membrane (Figs 5a, 6c). Bird-head avicularia present on the outer side of the zooids (Fig. 5a), with a downcurved beak (Figs 5a, 6b), and smaller than those of *B. stolonifera* (compare measurements in Suppl. material 1: table S8 and table S5). Average avicularium length equals average zooid width. Ovicells not seen. Ancestrula erect, elongate, may have 9 or 11 spines: three proximal, two lateral, and two or three pairs of distal ones (Fig. 5 showing 9 spines, but Fig. 6 showing 11 spines).

Remarks. The morphology of our specimens closely resembles the descriptions and drawings of *Bugula fulva* (=*Bugulina fulva* see Fehlauer-Ale et al. 2015) described

Figure 4. *Bugulina* cf. *fulva* from Coquimbo, Sample SCBUCN8180, whole specimen with proximal ancestrula.

from a harbour in Wales (Ryland 1960). *Bugulina fulva* has been recognized as a morphologically plastic species, exhibiting variation in the number of distal spines (Hayward and Ryland 1998). Examination of the holotype of *B. fulva* confirmed the presence of proximal spines, as first reported by Maturo (1966). Proximal spines were also observed in the specimens from Chile, although their number varied (Fig. 5a).

Despite the morphological similarities between the Chilean specimens examined in this study and the type specimens, we remain uncertain about the identification of our material. The Chilean specimens exhibit a greater number of proximal spines (1–2 inner and 1–3 outer) compared to the type specimens of *Bugulina fulva*, which are characterised by a single spine on the proximal outer edge of the opesia (observed only at the basal part of the colony in the type specimen). Interestingly, the Chilean specimens more closely resemble those reported from the Atlantic coast of the USA (Maturo 1966).

Figure 5. *Bugulina* cf. *fulva* from Coquimbo, Sample SCBUCN8180. **a.** Zooid with avicularia and latero-oral as well as lateral spines. **b.** Ancestrula with three proximal, two lateral and two pairs of distal spines.

On the other hand, recent characterizations of *Bugulina fulva* from other locations, such as the Madeira Archipelago (Ramalhosa et al. 2017), indicate the absence of proximal spines in this species. Additionally, at least three other *Bugulina* species may exhibit proximal spines: *Bugulina flabellata* (Thompson in Gray, 1848) (see Ryland 1960, fig. 9), *Bugulina ditrupae* (Hincks, 1886) (see Hincks 1886, Plate IX, figs 3, 4), and *Bugulina aquilirostris* (Ryland, 1960). A proximal spine in *B. aquilirostris* was not mentioned in the original description, but it was observed in the examined type material (NHMUK 1959.1.20.1). The specimens of *Bugula ditrupae* reported from Brazil by Marcus (1937) also exhibit proximal spines (see Marcus 1937: Plate XIV, fig. 36). However, this species was first synonymized with *Bugulina fulva* by Ryland (1960) and later with *Bugulina foliolata* by Vieira et al. (2012). As noted by Vieira et al. (2012), the morphological plasticity and distinctions between *B. fulva*, *B. aquilirostris*, and *Bugula ditrupae* (Busk, 1858) remain unresolved. A review of these species is beyond the scope of our study and requires further investigation.

Family Watersiporidae (Vigneaux, 1949)
Genus *Watersipora* (Neviani, 1896)

Watersipora arcuata (Banta, 1969)

Watersipora arcuata Banta 1969, figs 1–7; Mackie et al. 2006; 2012; Anderson and Haygood 2007; Ferrario et al. 2015, figs 3, 4; Reverter-Gil and Souto 2019, fig. 3; Gauff et al. 2023.

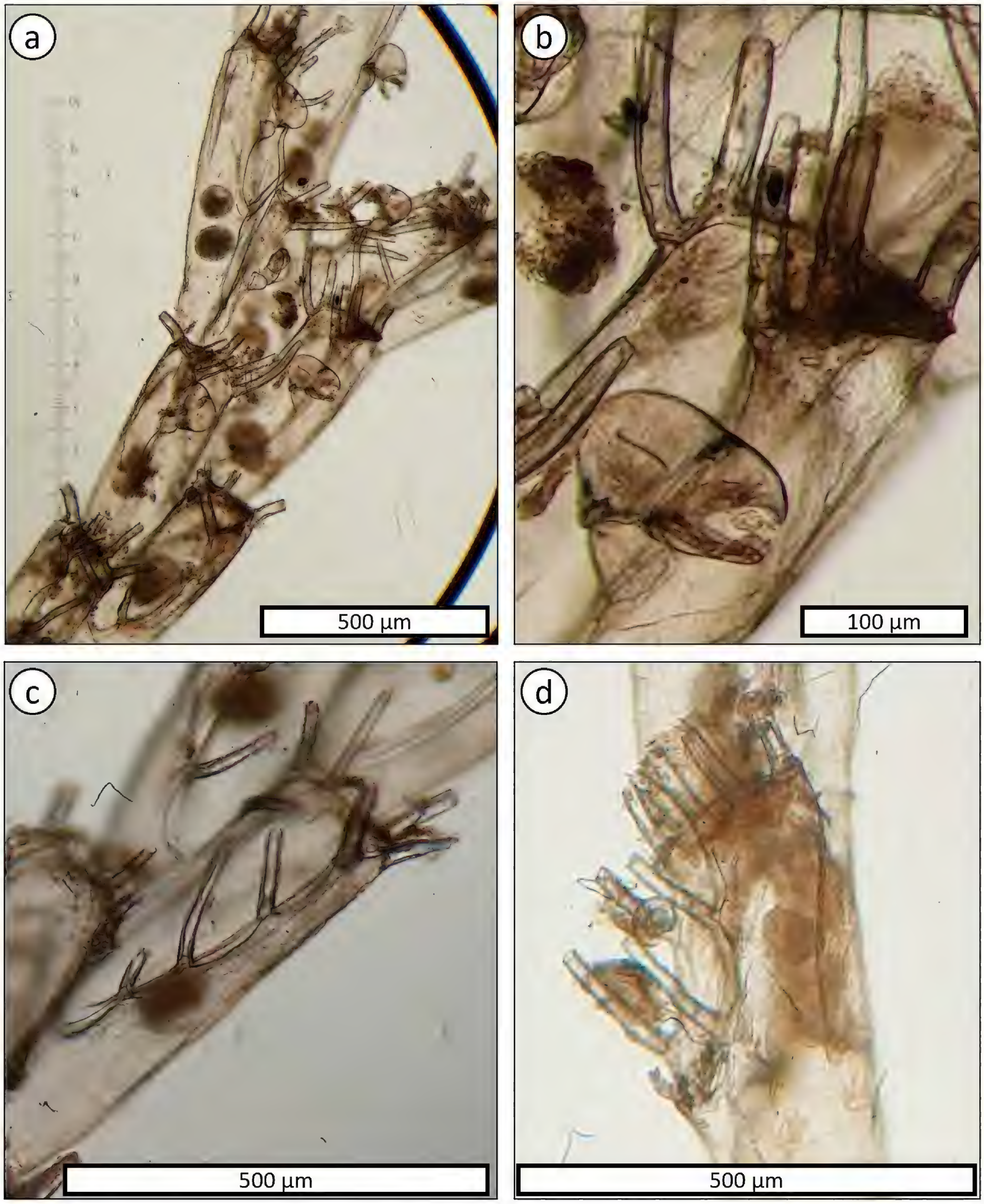

Figure 6. *Bugulina* cf. *fulva* from Coquimbo under light microscope. **a.** Zooids with distal spines, avicularia, and lateral spines (sample COQSUMBXS4). **b.** Close-up of an avicularium and distal spines (sample COQSUMBXS4). **c.** Close-up of one of the most proximal zooids of the colony, showing a zooid with three outer and three inner spines, with three additional outer spines at the inner opesial rim (sample 20240327sp2). **d.** Ancestrula with three pairs of distal spines and two pairs of lateral spines (sample 20240327sp4.5); the median proximal spine is missing.

Material analysed. SCBUCN 8181, Genbank PP109397, growing on a piece of cement-stone conglomerate, collected 2 September 2023 and **SCBUCN 10539**, growing on a natural stone, collected 3 July 2024. Both samples from the rocky

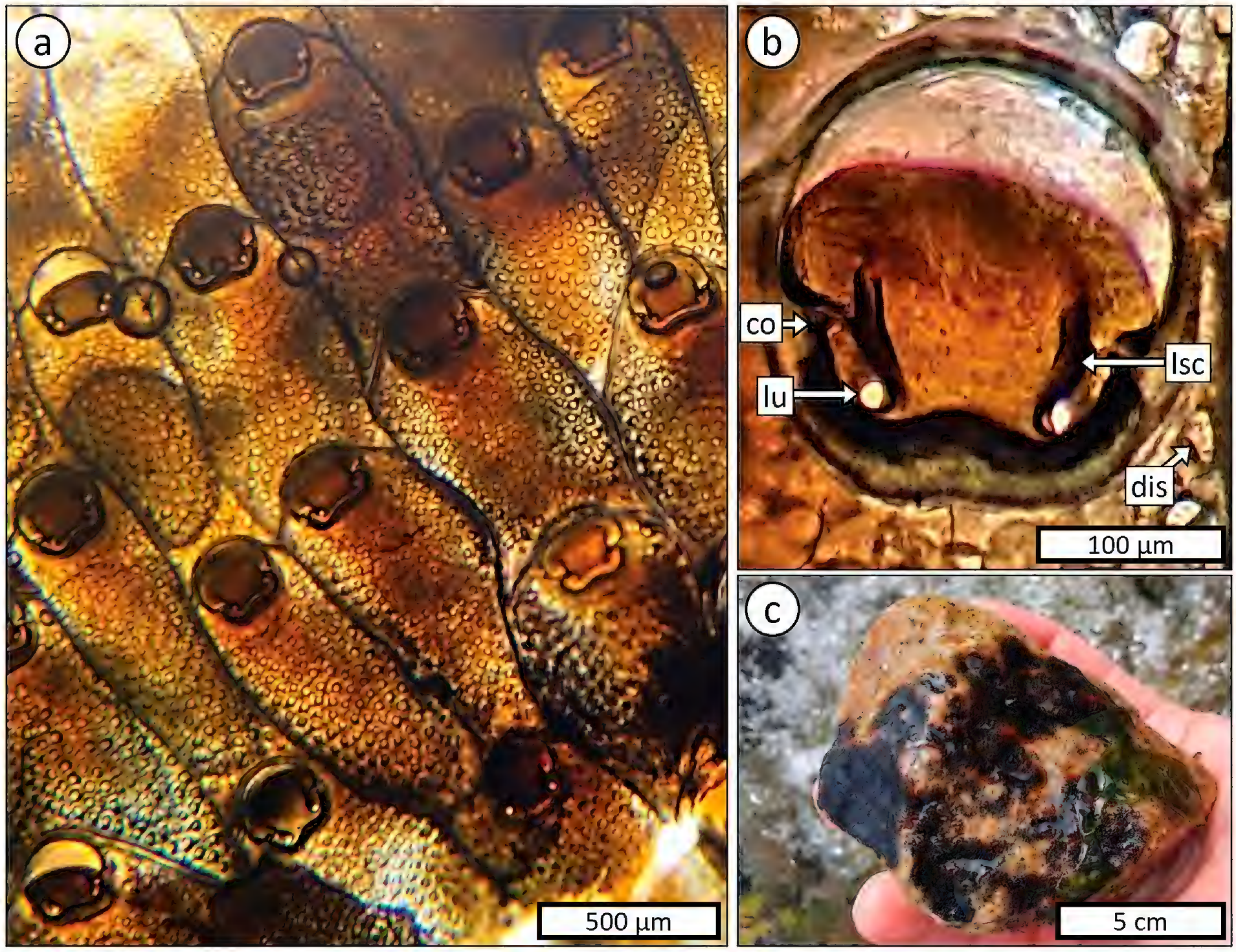

Figure 7. *Watersipora arcuata*, sample SCBUCN8181. **a.** Several zooids photographed under light microscope. **b.** Operculum with condyles (co), lateral sclerites (lsc), lucidae (lu), and distal intrazooidal septulum (dis). **c.** Colony encrusting stone from the upper intertidal zone at the sampling site in Coquimbo.

intertidal (depth: 0–0.10 m) adjacent to an artificial pier at Campus Guayacán of Universidad Católica del Norte in Coquimbo, Chile (29.97°S, 71.35°W). The site is in close proximity to the local fishing port (linear distance: < 300 m) and an anchorage site for large commercial vessels from the local mining industry (linear distance: < 500 m; Fig. 1b).

Comparative material analyzed. USNM RB 8495, *Pachycleithonia nigra* Canu & Bassler, 1930, Galapagos.

Characterization. Colonies black, with reddish edges (Fig. 7c), up to 10 cm in extension, firmly attached to the substratum. Zooids subrectangular to hexagonal, about twice as long as wide, with large variation even within a colony (Fig. 7a). Frontal wall with about 150 pseudopores of 21 ± 2 µm in diameter (see measurements in Suppl. material 1: table S9). Orifice wider than long. Operculum with well-developed condyles, a pair of lateral sclerites and two lucidae (Fig. 7b). Distal intrazooidal septula visible under light microscope (Fig. 7b). Distal and posterior septula present (Fig. 8). Intrazooidal septulum visible on the lateral vertical wall of one zooid (Fig. 8d). No spines or avicularia. Embryos lacking in examined material.

Remarks. In the Southeast Pacific, *Watersipora arcuata* is only known from the Galapagos Islands, about 1000 km off Ecuador (Banta 1969). Two more congeneric species, *W. subtorquata* (Rech et al. 2024a) and *W. nigra* (Vieira et al. 2014) occur

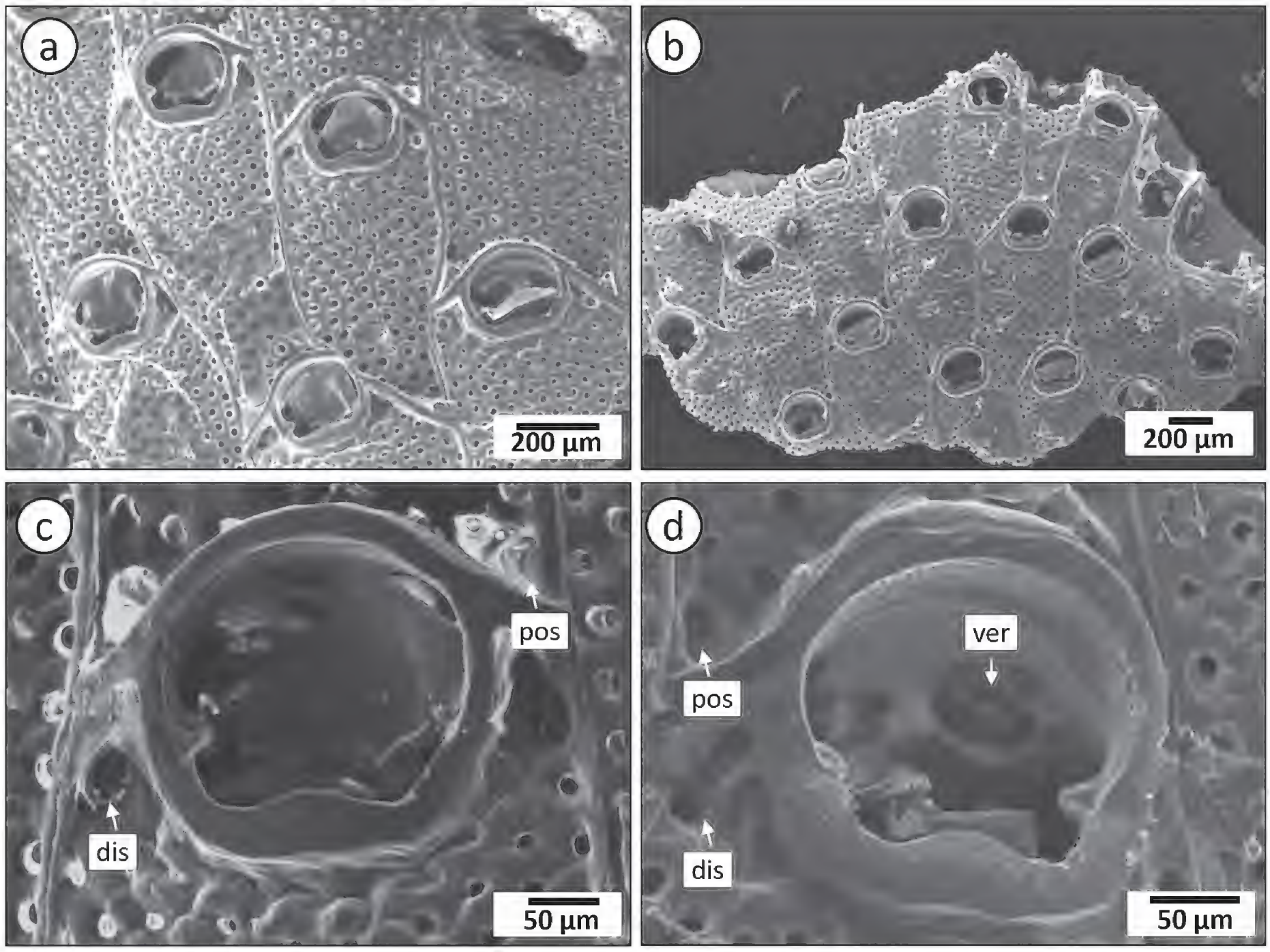

Figure 8. *Watersipora arcuata*. samples SCBUCN8181 (**a, c**), and sample SCBUCN10539 (**b, d**). **a, b.** Colony overview; **c, d.** Orifice with intrazooidal septula: dis = distal, pos = posterior, ver = vertical.

in the Southeast Pacific. *W. arcuata* differs from both in the presence of paired distal intrazooidal septula. Moreover, *W. subtorquata* and *W. nigra* are respectively characterised by a U-shaped and squared sinus (see Rech et al. 2024a for *W. subtorquata* and Suppl. material 1: fig. S5 for *W. nigra*), while *W. arcuata* has a more rectangular sinus (Fig. 8 c, d). Visual identification of our specimens as *W. arcuata* is corroborated by genetic analysis. Our material is highly similar (98 – 100% similarity) to published COI sequences from the Northeast and Southwest Pacific (California, Hawaii, Australia; see Suppl. material 1: table S10).

Discussion

Patterns of species richness and community composition

We detected a total of sixteen bryozoan species, including eleven non-indigenous or cryptogenic species, along the Chilean coast using a combined approach of standardised settlement plate-based surveys and additional records. This includes three new species records for Chile. Considering the low number of known NIS on the Chilean continental coast (e.g., Stowhas et al. 2023), these additions represent a significant update to the local non-indigenous fauna. Despite site and season-related differences in species richness, there was no overall geographic or seasonal pattern. Each study site had a characteristic individual compositional profile, and

the highest environmental and geographic dissimilarity coincided with the highest dissimilarity in community composition. This was seen for oceanic Rapa Nui, which shared no species with the continental sites and for the only estuarine site, Ancud, where species composition had the least similarity with all other continental sites. These dissimilarities may be based on geographic factors, like distance to the mainland (for Rapa Nui), or environmental conditions, like salinity (for Ancud) or water temperature. Other factors influencing (invasive or cryptogenic) species richness and composition may be the intensity of long-distance and local vessel traffic, as well as the presence and abundance of fouling fauna already present at the respective site (see Leclerc et al. 2020a). Despite these considerations, the bryozoan species analysed here were part of a more diverse fouling community growing on settlement plates at each sampling site, which may influence the richness and abundance of our target species through ecologic interactions. Therefore, the present study, which is focussed on a taxonomic description of non-indigenous Bryozoa, was not designed to and cannot discern the causes of the observed differences.

NIS introduction

Vessel traffic is one of the most common vectors for marine invasions (e.g., Castro et al. 2020; Bailey et al. 2020), with ports serving as key sites for NIS introduction (e.g., Leclerc et al. 2018; Pinochet et al. 2023; Rech et al. 2024a). In fact, 30–40% of Chilean NIS, including the bryozoans *Bugula neritina* and *Bugulina* cf. *flabellata*, are considered to be ship-borne introductions (Castilla and Neill 2009). This is likely also the case for the newly reported non-indigenous and cryptogenic species in our study, which are typical constituents of marine fouling communities and were found in ports and marinas. However, identifying the vector and geographic source of an introduction can be challenging, particularly when it is unclear how long a NIS has been present at a site before detection. This is true for the two newly recorded species, *Bugulina* cf. *fulva* and *Bugulina stolonifera*, both of which are easily confused with the widespread *Bugulina* cf. *flabellata* in rapid field surveys without microscopic analysis and may have gone undetected for extended periods.

A noteworthy finding in our study is the discovery of *Watersipora arcuata* in the rocky intertidal zone at the Coquimbo site. This site is frequented by students from the adjacent Faculty of Marine Sciences and was also visited during a marine bioinvasions workshop in 2019. However, *W. arcuata* was only detected in September 2023, when students identified distinctive black patches with reddish edges covering the intertidal rocks and stones. The colonies were abundant and easily visible at low tide, suggesting that this is a recent introduction (likely within the last five years). The invaded site is located near the local mining port for international cargo vessels, where an average of 23 vessels arrived annually between 2019 and 2023. Most of these vessels came from Asian countries (66%), particularly China and South Korea (Suppl. material 1: table S11), and stayed in port for an average of 7 days. Vessels from South America and Central America also arrived, though with lower frequencies (24% and 10%, respectively), and shorter stays (Suppl. material 1: table S11).

Considering the nature of *W. arcuata* as a typical fouling species and the location of the colonies, it seems likely that this species was introduced via internationally travelling vessels arriving at the mining port. However, the native range of *W. arcuata* is unknown, and it has not been recorded from Asia, mainland South America, and Central America in the scientific literature. While there are records

of *W. arcuata* from the US East Coast (Vieira et al. 2014), only one of the 115 vessels arriving at the Guayacán terminal between 2019 and 2023 came from that region. Therefore, given the lack of overlap between the known distribution of *W. arcuata* and the origin of the vessels arriving at the Guayacán terminal, we cannot confidently infer the geographic origin of the colonies found in Coquimbo, Chile.

Establishment and local dispersal

Ports not only serve as important entry points for NIS, but they also provide ideal habitats for these species after their introduction. In fact, Leclerc et al. (2020a) observed that the high colonisation success of NIS on settlement plates was independent of international vessel traffic, indicating that these species had already established in the respective ports. This is likely due to the abundance of artificial infrastructure, particularly floating structures, which offer settlement opportunities and protection from benthic predation for newcomers (Dumont et al. 2011; Leclerc et al. 2020b; Rech et al. 2024b). In contrast, NIS colonisation of benthic settlement plates (Leclerc et al. 2020a) or even adjacent natural benthic environments (e.g., Forrest et al. 2013; Simkanin et al. 2013) tends to be less frequent.

The discovery of *Watersipora arcuata* in the intertidal zone at the Coquimbo site is concerning. Unlike many other NIS, *Watersipora* species have invaded rocky intertidal and subtidal habitats, as well as coastal reefs in Northeast Pacific California (Zabin et al. 2018; Page et al. 2019), likely dispersing from local ports and marinas. Over shorter distances (< 4.5 km), larval connectivity with the nearest port has been suggested as a dispersal mechanism (Page et al. 2019). However, over longer distances, secondary dispersal of NIS is often facilitated by locally operating recreational boats (e.g., Davidson et al. 2010; Ashton et al. 2022a). In the small Bay of Coquimbo, with a maximum width of 2 km, larvae could easily spread naturally. Additionally, artisanal fishing boats and other leisure craft are frequently anchored near the invaded site, posing a significant risk of further dispersing the species along the coast.

At our study site in the temperate SE Pacific, *W. arcuata* was present on the seafloor, where predation pressure is strong, but not on settlement plates floating in the water column (at a distance of only 100 m from the invaded site), where predation is virtually absent (see Dumont et al. 2011; Rech et al. 2024b). This finding is most likely explained by a facilitating effect of benthic predation on *Watersipora* establishment. On the floating settlement plates, where there is no predation pressure, a dense and diverse fouling community, largely dominated by *Ciona robusta* and other ascidians (unpublished data, but see photo in Suppl. material 1: fig. S1), exerts biotic pressure through competition and may inhibit *Watersipora* establishment. On the seafloor, on the other hand, high predation pressure through (mainly) benthic crabs and fishes (see Musrri et al. 2019) impedes the growth of soft-bodied species with no structural defence mechanisms like *Ciona* (e.g., Dumont et al. 2011; Giachetti et al. 2020). *Watersipora arcuata*, in contrast, is protected from predators due to its flat, encrusting form and calcareous skeleton, and can spread more effectively when competing species are removed by predators (Oricchio and Munis Diaz 2020; Chebaane et al. 2023). Biotic facilitation of *Watersipora* species through predation has also been documented in other studies: Needles et al. (2015) observed increased abundances of *W. subtorquata* in the presence of sea otter and sea star predators that removed the competing foundation species *Mytilus californianus*

in a Californian bay. Similarly, Chebaane et al. (2023) found that abundances of *W. subatra* on settlement plates were higher in open (= predator-accessible) than in caged (= predator-excluding) treatments in two Portuguese marinas.

Another significant finding of our study was the detection of *Bugulina stolonifera* at three different sites, spanning a total distance of 1,300 km from Coquimbo to Puerto Montt. This suggests that the species may already be well established in Chile. However, we cannot yet determine if there is any connectivity between the colonies across these different study regions or how many individual introductions have contributed to their spread. Population genomics have been used to assess inter-populational relationships of marine NIS in previous studies (e.g., Page et al. 2019) and could be an important tool to elucidate the invasion history of *B. stolonifera* in Chile.

Recommendations for monitoring and prevention

Two of the three newly reported species were detected through settlement plates deployed at strategically chosen high-risk sites over a relatively short period of just four months. Settlement plate-based surveys are widely used worldwide for detecting NIS (e.g., Tamburini et al. 2021) and have been successfully implemented in Chilean continental ports (Leclerc et al. 2018, 2020a,b), as well as on the remote island of Rapa Nui (Easter Island; Rech et al. 2024a). The relatively high number of previously unreported species found in our study, despite including only seven sites, suggests that many other NIS may remain undetected in other locations, both within Chile and in other understudied regions globally. This highlights the potential of settlement plates as a promising tool for future NIS detection in such areas.

As noted in this study, visual identification of bryozoans at the species level is challenging and often necessitates scanning electron microscope (SEM) images. Visual identification in the field is frequently ambiguous, as similar species can easily be confused or overlooked. This is likely the case for *B. stolonifera* and *Bugulina* cf. *fulva*, both of which may have been misidentified as the congener *Bugulina* cf. *flabellata* in previous studies. Given these new findings, a comprehensive genetic and morphological analysis of the genus *Bugulina* in Chile will be crucial to clarify which species are present and how they are distributed. Unambiguous identification of NIS bryozoans in Chile is essential for understanding their introduction pathways and implementing effective prevention and control measures.

Hull fouling plays a critical role in the introduction of NIS, prompting several countries and regions, such as California and New Zealand (Scianni et al. 2021), to implement regulations targeting vessels arriving in their territories. However, such legislation is still lacking in most parts of the world. In Chile, with over 5,000 international vessel arrivals annually (Stowhas et al. 2023), the only study conducted on hull fouling so far has found several NIS attached to arriving international vessels (Pinochet et al. 2023), and Chilean ports are recognized as hotspots for marine invasions (e.g., Leclerc et al. 2018, 2020a,b). Despite the relatively low number of reported marine NIS to date, models predicting shipping frequencies suggest a significant increase of 15 to 35 NIS arriving per year (Sardain et al. 2019). Interestingly, a number of previously unreported NIS have been identified in Chile during the past decade, including several species in Coquimbo (Häussermann et al. 2015; Beermann et al. 2025). While Chile has begun preparing measures to mitigate hull fouling-related bioinvasions (Stowhas et al. 2023), no legislation is yet in place. It is imperative that such regulations be implemented to safeguard Chile's coastlines from future invasions.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

All procedures involving animals were in compliance with the European Community Council Directive of 24 November 1986, and ethical approval was granted by the Ethics Committee of Universidad Católica del Norte (CEC UCN N° 07/ 2020, Coquimbo, Chile). On Rapa Nui, permit for the study was granted by Koro Nui o te Vaikava o Rapa Nui (Consejo del Mar de Rapa Nui; Permit N°3_2022).

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Author contributions

SR: Conceptualisation, Methodology, Formal analysis, Investigation, Data curation, Writing – original draft, Visualisation, Project administration, Funding acquisition. LMV: Investigation, Validation, Writing – review and editing. AIV: Investigation, Methodology, Writing – review and editing. MSRB: Investigation, Methodology, Writing – review and editing. JPF: Investigation, Resources. DPG: Validation, Writing – review and editing. MCS: Investigation. KP: Resources. JS: Resources. MT: Conceptualisation, Methodology, Resources, Supervision, Funding acquisition, Writing – review and editing.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

Supplementary tables and figures

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